

# On the identity of *Pleurosigma angulatum* (Bacillariophyta) and related species

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**SYNOPSIS.** The specific status of *Pleurosigma angulatum* (J.T. Quekett) W. Sm. is clarified. *P. angulatum*, *P. quadratum* W. Sm. and *P. aestuarii* (Bréb.) W. Sm. are shown to be separate taxa. Recent research has subsumed the three taxa under the epithet *angulatum* on the basis that they may occur together and so may represent different stages in the life cycle of one species. The results of this study show this is clearly not the case.

Two new species of *Pleurosigma* are described; *P. mamoranqi* **sp. nov.** from New Zealand and *P. lysekilii* **sp. nov.** from Sweden. One new name, *P. malmoensis* **nom. nov.**, is given to the taxon previously called *Pleurosigma minutum* (Grun.) Cl.

## INTRODUCTION

The genus *Pleurosigma* W. Sm. is a member of the family Pleurosigmataceae. *Pleurosigma* is a readily recognized genus owing to its large size, sigmoid outline or sigmoid raphe, and its arrangement of transverse and oblique striae. It has two or four ribbon-like plastids which undulate throughout the cell. Initially, species of *Pleurosigma* were distinguished largely on the basis of their shape (Kützing, 1833; Ehrenberg, 1838; Rabenhorst, 1853).

Smith (1852) used the new name *Pleurosigma* W. Sm. for sigmoid naviculoid diatoms; his reason for rejecting the earlier name *Gyrosigma* Hassall, which was in his view synonymous with *Pleurosigma*, was that it was an 'alliterative blunder' (Smith, 1856: 97). Smith (1852) introduced additional taxonomic criteria in this group of diatoms by separating species into two 'sections' on the basis of the arrangement of the striae. He also provided details of the stria density for each species and used this as the basis for discriminating between them. Smith's (1852) two sections reflected the modern concepts of *Gyrosigma* and *Pleurosigma*, his first section being described as having 'Beads alternate, striae oblique', i.e. *Pleurosigma* (Round et al., 1990), whereas his second section had 'Beads opposite, striae transverse and longitudinal', i.e. *Gyrosigma* (Round et al., 1990).

Peragallo (1891) investigated the angle of intersection of the

striae in taxa of the family Pleurosigmataceae. By combining the angle of intersection and fineness of the striae, he was able to discriminate additional species and divide them into 11 groups; *Pleurosigma* was still included within *Gyrosigma* at this point. Cleve (1894) later separated *Gyrosigma* from *Pleurosigma* using the orientation of the striae and assessed species limits within the genera by the shape and path of the raphe.

*Pleurosigma angulatum* (J.T. Quekett) W. Sm. was conserved as the type of the genus *Pleurosigma* by Ross (during the 8th International Botanical Congress, Paris, 1954). *P. angulatum* has been treated in a variety of ways encompassing a large number of varietal forms (16 listed in Reid, 1998). It was first described by Quekett (1848:438) as *Navicula angulata* from 'the Humber at Hull'. Recent work by Sterrenburg (1991a) and Ross & Sterrenburg (1996) argued that *P. angulatum* be extended to encompass *P. angulatum*, *P. quadratum* W. Sm. and *P. aestuarii* (Bréb.) W. Sm. This was based on the assumption that they are all part of the same species, just exhibitions of different stages in the 'vegetative cycle of a single organism; *quadratum* as early stage, *angulatum* representing mid-range and *aestuarii* as late stage' (Sterrenburg, 1991a: 564). Searches for Quekett's original material failed to locate any specimens and resulted in the proposal to conserve the name *P. angulatum* (J.T. Quekett) W. Sm. with a conserved type slide from the Wm. Smith collection (BM 23671) (Ross & Sterrenburg, 1996).

In a detailed monographic study of the genus *Pleurosigma*, Reid

(1998) disagreed with Sterrenburg's findings. Her results showed that *P. angulatum*, *P. quadratum* and *P. aestuarii* should be recognized as separate taxa. This study extends Reid's (1998) findings using cladistic analyses to explore the relationships of the three taxa and their close relatives as indicated from Reid's results.

## MATERIALS & METHODS

Slides were examined using a Reichert microscope. For photomicroscopy, specimens were examined on a Carl Zeiss microscope, with differential interference contrast, using plan apochromat objectives and tri colour green filter. Photos were taken using medium format Kodak Tmax 100 film. Cleaned specimens were strewn on aluminium stubs for SEM examination. The specimens were sputter coated with platinum and observed using a Hitachi S800 field electron microscope. All slides, negatives and SEM stubs of the specimens are housed in the herbarium of The Natural History Museum, London (BM).

## Diatom morphology

Terminology for the siliceous parts of the diatom frustule follows that of Anon. (1975) and Ross et al. (1979).

Characters that appeared constant within species were investigated using cladistic analysis. Character stability was established by investigating about ten populations from each taxon (examining more than 100 individuals from each population) for infra- and inter-specific variation. Individuals were cultured from each population and subjected to variations in temperature (9–30°C), salinity (7–43 ppt) and light (8–45  $\mu\text{mol m}^{-2} \text{sec}^{-1}$ ) to assess character stability under a multifactorial design. All characters were measured in both the 'wild' and the 'cultured' material.

Only qualitative characters were used in the cladistic analysis. Quantitative characters were not used due to the inherent problems of coding continuous characters into discrete states for analysis (Pimentel & Riggins, 1987; Thiele, 1993; Reid & Sidwell, 2001). Many characters traditionally associated with diatom valve morphology are quantitative (e.g. length, breadth, stria ratios) and only used in species descriptions. The only characteristics of shape that can be used qualitatively are first, the broad definition of cells as arcuate (as in the outgroup *Toxonidea* Donkin, compared to sigmoid cells as in the remaining *Pleurosigmataceae*), and second, shape in girdle view (oblong in *Pleurosigma* and panduriform in *Donkinia*).

Within the family *Pleurosigmataceae* the striae are arranged in one of two ways; transverse and oblique rows in *Pleurosigma*, *Toxonidea* and *Donkinia*, longitudinal and transverse rows in *Gyrosigma* and *Donkinia*. This character was first used to separate *Gyrosigma* and *Pleurosigma* into two distinct genera by Cleve (1894). The areolae in the *Pleurosigmataceae* are loculate and occluded by a rima. The areolae open externally by a slit, the foramen. The internal areola opening in the *Pleurosigmataceae* can be divided into two types; either a single opening which is found in *Gyrosigma*, *Toxonidea*, some species of *Pleurosigma* (Fig. 3c) and *Donkinia*, or areolae divided by a siliceous bar, as found in some species of *Pleurosigma* and *Donkinia* (Fig. 5c). In some species of *Pleurosigma* the striae change orientation near the apex of the valve from the transverse/oblique pattern to the transverse/longitudinal pattern (Fig. 3f). This change was first noted and clearly drawn and discussed by Anthony (1870). Sterrenburg attributed this discovery to Hendey (1964), commenting that 'this had never been described or drawn in the previous century of observations' (Sterrenburg, 1991a:561). This is not the case, as it had been commented on frequently in the literature

prior to Hendey, for example Brown (1914:327) regarded this as 'a good specific character', and Woodward (1871:160) made detailed photographic illustrations of the character.

The external central raphe fissures of *Pleurosigma* were first discussed as a taxonomic character by Cardinal et al. (1989). These are continuations of the external raphe slit opening, extending onto or across the central nodule, but not penetrating the valve. This character refers to the orientation of the central external raphe fissure endings (see Fig. 2g). Cardinal et al. (1989) used six character states in their study, only four of these are seen in the species under investigation here: either the central fissures are curved in opposite directions, similar directions, one centered and the other deflected, or the central fissures are overlapping.

Central bars are siliceous thickenings deposited either side of the internal central nodule (Fig. 2f). Reid (1998) observed eight character states in her study, four of which are observed in the species under investigation here: central bars smooth and slender, with an indistinct hazy edge, with siliceous lateral extensions or thick and raised. A hyaline area may occur adjacent to these bars (this is an area which is not penetrated by areolae) and may follow the shape of these bars (Fig. 3h) or be transversely expanded (Fig. 5c) or absent (Fig. 2f). In some species of *Pleurosigma* the internal central area is raised to form a 'saddled' humped area. The internal central nodule may have an extra siliceous deposit in the centre in some species of *Pleurosigma* (Fig. 5c), a character referred to as 'central nodule raised' in the cladistic analysis.

## Analysis

Table 1 lists the characters and the character states used in the analysis; character coding is presented in Table 2. The data set

**Table 1** Characters and character codes used in the cladistic analysis

Character	Character Description	Character code
0	Valve arcuate	0
	Valve sigmoid	1
1	Striae transverse and oblique	0
	Striae transverse and longitudinal	1
2	Raphe arcuate	0
	Raphe sigmoid	1
3	Areolae undivided	0
	Areolae divided	1
4	Striae same orientation at apex	0
	Striae change orientation at the apex	1
5	Central raphe fissures:	
	Curved in same direction	0
	Curved in opposite directions	1
	One centred the other deviated	2
	Overlapping	3
6	Central area not saddled	0
	Central area saddled	1
7	Central bars:	
	Smooth and slender	0
	With indistinct hazy edge	1
	With siliceous lateral extensions	2
	Thick and raised	3
8	Hyaline area:	
	transversely expanded	0
	follows the central bars	1
	absent	2
9	Central nodule raised	0
	Central nodule plain	1
10	Valve flat	0
	Valve vaulted	1
11	Girdle view oblong	0
	Girdle view paduriform	1

**Table 2** Data matrix used in the cladistic analysis

	0	1	2	3	4	5	6	7	8	9	10	11
<i>Toxonidea</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. angulatum</i>	1	0	1	0	1	2	0	1	2	0	0	0
<i>P. quadratum</i>	1	0	1	0	1	2	0	1	1	0	0	0
<i>P. aestuarii</i>	1	0	1	0	1	3	0	0	2	1	0	0
<i>P. stidolpii</i>	1	0	1	0	0	3	0	2	0	1	1	0
<i>P. mamorangi</i>	1	0	1	1	0	3	0	0	0	0	0	0
<i>P. lysekilii</i>	1	0	1	?	0	0	0	0	?	?	0	0
<i>P. malmoensis</i>	1	0	1	?	0	0	0	0	?	?	0	0
<i>P. rhombeum</i>	1	0	1	0	0	1	1	0	0	0	1	0
<i>D. minutum</i>	1	1	1	0	0	?	0	3	1	1	1	1
<i>D. latum</i>	1	1	1	0	0	?	0	3	1	1	1	1

contains ten binary characters and two multistate characters, which were coded with reference to *Toxonidea* as an all zero outgroup (Nixon & Carpenter, 1993).

*Pleurosigma minutum* Donkin (not to be confused with *Pleurosigma minutum* Grun.) is synonymous with *Donkinia minutum* (Donkin) Ralfs. As *Donkinia* is seemingly closely related to *Pleurosigma*, two species in the genus, *D. minutum* and *D. latum* E.J. Cox, were included in the analysis. *P. rhombeum* Grun. was included in the analysis because this is a taxon which is often misidentified as *P. quadratum*.

Weighting is the importance applied to characters in analysis. When different characters are assumed to contribute to the same degree to the tree topology they are all given the same weight (uniform weighting), applied initially as the default in most current parsimony programs (e.g. Hennig86 – Farris, 1988; PAUP – Swofford, 1990). If the characters are assumed to contribute to different extents to the analysis they are given different weights (differential weighting).

In the past, weighting has tended to be a highly subjective process with intuition being the only basis for giving some characters more weight than others in an analysis (e.g. Mayr, 1969). Weighting may take place prior to tree construction, in which case it is termed *a priori* weighting (Neff, 1986), which takes into account what is known about the characters, or after initial tree construction, in which case it takes into account the contribution the characters make to the resulting tree topology, *a posteriori* weighting (Neff, 1986). *A priori* weighting is not appropriate as it is impossible to know which characters are useful before an analysis.

The first serious attempt to address the problem of how to weight characters was brought about by Farris (1969), but little use was made of it until he incorporated it into his computer program (Farris, 1988), as a differential *a posteriori* method. The method is based on the assumption that 'characters which have failed repeatedly to adjust to the expectation of hierarchic correlation are more likely to fail again in the future, and so they are less likely to predict accurately the distribution of as yet unobserved characters' (Goloboff, 1993a). In practice this is the same as excluding some characters and introducing the non-random replication of other characters. Farris's method (Farris, 1969, 1988) is iterative in that weights are applied to the most parsimonious trees for a given set of weights, and are then used in the reanalyses. It works on the basis that because the character consistency index (c) measures homoplasy but can never reach zero, by rescaling it with the retention index (ri) (which measures the amount of synapomorphy), characters with no synapomorphy can be disregarded in future analyses.

Goloboff (1991a) shows that Farris's method of weighting still has problems as weights do not always increase with less homoplasy. Goloboff (1993b) introduced a non-iterative method in which the weighting is based on a concave function of homoplasy, given as fit (f):

$$f = (k+1) / (s+k+1-m)$$

k = a constant of concavity, s = minimum number of steps a character can have on a particular tree, m = minimum number of steps a character can have on any tree. This is implemented using the computer program Pee-Wee (Goloboff 1993b) to analyse the data matrix. It selects trees of highest weight as being the most parsimonious, as opposed to the shortest total length, as under Hennig86 (Farris, 1988).

Some workers only advocate the use of weighting in the analysis if the initial unweighted data has failed to produce an adequate tree due to character conflict, or to choose between multiple trees (Turner & Zandee, 1995; Rodrigo, 1992). This approach is rejected here because weighting selects characters not cladograms. Many workers do not accept the concept of differential character weighting, arguing that every character should be attributed equal weight to create natural taxa because all characters are 'equally desirable' (Sneath & Sokal, 1973; Mann, 1982; Round et al., 1990). I shall use differential *a posteriori* weighting because it results in trees which are self-consistent with the data collected (Farris 1969, 1988; Goloboff, 1993a, 1995; Platnick et al., 1991), in that not all characters contribute equal amounts of information to the analysis. They are given the weight they deserve after initial analysis and thus weighting is required in all analysis.

Parsimonious trees for the data were found using Hennig86 (Farris, 1988) with the *ie\** command (implicit enumeration, which is guaranteed to find all the most parsimonious trees). Initially, all characters were given equal weight and were unordered. As it is possible that not all characters contribute to the same extent to the prediction of relationships (Farris, 1983; Goloboff, 1993a), *a posteriori* differential weighting was investigated (as implemented in the program Pee-Wee (Goloboff, 1993b)). The option *mult\*50* was used to search for trees of highest fit, performing random addition sequences of 50 replications each. Replication was followed by tree bisection and branch-swapping.

## RESULTS

Both Hennig86 and Pee-Wee resolved the same tree (length 19, ci 89, ri 88, fit 75 (Fig. 1)). The tree in Fig. 1 has seven nodes (labelled 0–6, with 0 the most basal node of the tree).

*Pleurosigma angulatum* and *P. quadratum* are resolved at node 4 supported by character 5 (central raphe fissure orientation) and character 7 (central bar type). Node 2 resolves *P. aestuarii* as sister taxon to these two taxa supported by character 4 (striae orientation at apex) and character 8 (hyaline area type). The resolution at node 3 (*P. rhombeum*, *P. stidolpii*, *D. minutum* and *D. latum*) is attributed to character 10 (valve vaulting). The resolution at node 5 (*P. stidolpii*, *D. minutum* and *D. latum*) is based on character 9 (central

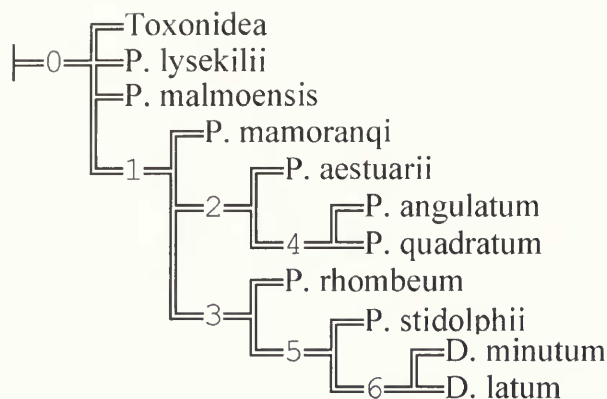


Fig. 1 Tree resolved by Hennig86 and Pee-Wee. Numbers on braches indicate the nodes

Table 3 Character weights

Character	Fit	Character	Fit
0	/	6	/
1	10	7	10
2	/	8	7.5
3	/	9	7.5
4	10	10	10
5	10	11	10

nodule type) and at node 6 (*D. minutum* and *D. latum*) based on character 1 (striae orientation), character 8 (hyaline area type) and character 11 (girdle view shape).

Weights attributed to the characters were high suggesting that they are relatively reliable (Table 3). Six characters received the maximum weight of 10, indicating that the characters were performing well and were hierarchically correlated. Two received a value of 7.5, which also indicates a high level of correlation. Characters 0 and 2 do not receive a weight because they only serve to separate the ingroup from the outgroup. Characters 3 and 6 do not receive a weight as they are autapomorphic.

## DISCUSSION

Sterrenburg (1991a: 561) stated that 'There is no morphological discontinuity between *Pleurosigma quadratum* W. Sm., *Pleurosigma angulatum* sensu W. Smith and *Pleurosigma aestuarii* (Bréb. ex Kütz.) W. Smith and the species description of *Pleurosigma angulatum* is extended to account for this continuum.' However, detailed morphological studies of large numbers of specimens has shown that this is not the case and that they are separate taxa.

The taxa differ in their hyaline areas; *Pleurosigma angulatum* and *P. aestuarii* do not have one (Figs 2f & 4c) whereas in *P. quadratum* the hyaline area follows the central bars (Fig. 3h). The taxa differ in their central bars, with *P. quadratum* having extra thickening at the centre of the bar (Fig. 3h) whereas *P. angulatum* has a more even deposit of silica (Fig. 2f) and *P. aestuarii* has smooth slender bars (Fig. 4b). *P. quadratum* is a much larger taxon than *P. angulatum* with a distinctive rhomboidal shape, compared to the more lanceolate form of the latter species. *P. aestuarii* is much smaller with rostrate ends. *P. angulatum* possesses a different pattern change at its apices to *P. quadratum* and *P. aestuarii*. On the outside curve of the

raphe the pattern continues approximately twice as far as on the opposite side (Figs 2h-j), whereas in *P. aestuarii* and *P. quadratum* the change in stria orientation is equal on both sides of the raphe (Figs 3b, c, f & 4c). Due to these differences they are maintained as separate taxa.

The basis for Sterrenburg's (1991a) summation is that the taxa are frequently found together. In this study, examination of many different populations showed that this is not the case, with their only occasionally being found together. While in nature many taxa frequently occur together, this is no basis for assuming that they are all to be regarded as one taxon; they may just have similar environmental requirements. Sterrenburg (1991a: 564) considers that there is 'a biological continuum between *quadratum*, *angulatum* and *aestuarii*'. Yet he admits that 'some samples may be almost pure *aestuarii*', continuing that 'While this may suggest the taxon's individuality, it does not necessarily imply it'. Reid (unpublished data) grew populations of *Pleurosigma angulatum* under different environmental conditions and monitored their morphometric changes. She found no evidence to support Sterrenburg's hypothesis.

Sterrenburg (1991a: 563) states that 'central bars were found to be highly variable in several of the "states" defined and discussed in Cardinal et al. (1989).' This found central bars to be a stable character both within a population and between populations from different sites. As Sterrenburg is subsuming the taxa under one species this may account for the variability he is observing. Sterrenburg (1991a) also sees the three taxa as part of a size range continuum. If this is the case, why is there a complete size range for each species that can clearly be seen to belong to each nominate type? Examination of large populations from different locations reveals the range in variation, but each taxon can still be clearly recognized.

Sterrenburg (1991a) suggested that Queckett (1848) had illustrated two taxa because his illustrations show one taxon with 51° and one with 60° angle of stria intersection. However this does not necessarily imply the inclusion of two different taxa, because this range of angles can be found in *Pleurosigma quadratum*, which exhibits angles from 50–60°. This is a continuous character, which cannot be fitted into discrete character states. Sterrenburg (1991a) refutes this possibility as 'Stria angle was found to be a stable parameter in this genus in Sterrenburg 1991 and the findings then indicated that 51 deg. falls outside the range of variation for *Pleurosigma angulatum* sensu W. Smith.' (Sterrenburg, 1991a:561). These observations were made on only two populations, one from the Wadden Sea, Holland and one from New Zealand (Sterrenburg 1991b:371) so it is quite likely that the full range of variation was not observed, giving him only 57–62°.

However, the results of the systematic analysis do show these taxa to be closely related. *Pleurosigma angulatum* and *P. quadratum* are resolved in both the unweighted and the weighted analyses as sister taxa (Fig. 1) at node 4 supported by character 5 (central raphe fissure orientation) and character 7 (central bar type). *P. aestuarii* is shown to be their closest relative at node 2 supported by characters 4 (striae orientation at apex) and 8 (hyaline area type). The shift in orientation at the apex was discussed by Reid (1998) and has been shown to be a stable taxon-specific character within the genus *Pleurosigma*. This character is a very useful aid to the identification of this complex group as it is easily visible under the light microscope and is shown by only 15 members of the genus. It does not change under environmental conditions or during growth.

No unmounted material was available for SEM investigation of *Pleurosigma lysekilii* Reid and *P. malmoensis* Reid, therefore characters 3 (areolae type), 8 (hyaline area type), and 9 (central

nodule type) are scored as '?' in the cladistic analysis, leaving them unresolved within the group at node 0 of the tree (Fig. 1).

*Pleurosigma mamoranqi* Reid differs from *P. angulatum*, *P. quadratum* and *P. stidolphii* Sterrenburg in having areolae crossed by a bar. It differs from *P. angulatum* and *P. quadratum* by its striae that do not change orientation near the apex. It has a large expanded hyaline area adjacent to the central bars. It differs from *P. rhombeum* by not having a saddled central area. This taxon does not fit any of the previously published descriptions of *Pleurosigma*, and as such is described as new.

In the first part of his monograph Peragallo (1891:12) considered *Pleurosigma minutum* to be a valid taxon and expands its distribution from Malmö, Sweden to include the Balearic Islands. However, in the second part of his monograph, Peragallo (1891:34) considers *P. minutum* as a doubtful or unknown species. He says 'Je n'ai pu l'identifier avec certitude.' (Peragallo, 1891:34). The present study shows that *P. minutum* is a valid taxon that can be clearly distinguished from other species of *Pleurosigma*. *P. minutum* is quite different to *Donkinia minutum* which has a highly vaulted valve with its raphe on a keel. It is panduriform in girdle view whereas *P. minutum* is rectangular. *P. minutum* has transverse and oblique striae whereas *D. minutum* has transverse and longitudinal striae. However, as the name *P. minutum* had been used prior to Grunow (*P. minutum* Donkin, 1858:24, 3/9) a new name, *P. malmoensis*, is proposed for this taxon. *D. minutum* was not shown to be closely related to *P. malmoensis*, being placed in a different part of the tree, and therefore they cannot be considered as the same taxon.

## TAXONOMIC TREATMENT

1. *Pleurosigma angulatum* (J.T. Quekett) W. Sm. in *Ann. Nat. Hist.* 9: 7, pl. 1 fig. 8 (1852) Type: England, Hull, Humber Estuary (Lectotype: Belfast, 1996, Ross & Sterrenburg BM 23671!).

Fig. 2

*Navicula angulata* J.T. Quekett in *A practical treatise on the use of the microscope*: 438, pl. 8 fig. 4–7 (1848).

*Pleurosigma angulatum* f. *minor* Rabenh., *Flora Europea Algarum*: 234 (1864).

*Pleurosigma angulatum* var. *robustum* McCall, *J. Linn. Soc., Botany* 49: 265, 306 (1933).

Valve rhomboidal sigmoid, length 120–280 µm, breadth 30–35 µm (Figs 2a–d). Raphe sigmoid, central, becoming slightly eccentric near the apices (Figs 2a–d). External central raphe fissures with one centred and the other deflected to one side (Fig. 2g). Hyaline area absent (Fig. 2e, f). Striae 20 per 10 µm, crossing at an angle of 54–60°. Striae change orientation at the apex, the pattern change continues about twice the distance on the outer most curve of the raphe compared with the inner side (Figs 2h–j). Areolae undivided. Central bars of approximately equal length with an indistinct outer edge (Fig. 2f).

Ross & Sterrenburg (1996) chose to conserve BM 23671 as the type of the species. They record it as 'Belfast, August 1849', and state that this slide is from a locality listed in Smith (1853:65) 'Poole Bay, Aug. 1848; Belfast Bay, Aug. 1849; Coast of Sussex, April, May and Aug. 1852, W. Sm. Coast of Lancashire, Mr. Johnson. Rye, Mr. Jenner. Hull, Mr. R. Harrison. Coast of Norfolk, Mr. Brightwell'. This is somewhat misleading because in his earlier work, when he originally described *P. angulatum*, Smith (1852) gave the locality as Belfast Bay, Liverpool not Belfast (Ireland). The choice of locality

is also somewhat strange as Quekett's (1848) original description is of a taxon found 'upon conferva in the Humber at Hull'. From the list in Smith's (1852) description ('Poole Bay; Belfast Bay, Liverpool; Coast of Sussex, &c.; Coast of Lancashire, Chr. Johnson, Esq.! Rye, Mr. Jenner! Hull, Mr. R. Harrison! Norfolk, Thos. Brightwell Esq.!' (Smith 1852:7)) a Hull sample would have been a more judicious choice, for example BM 11809 and BM 11810 both from Hull and collected by R. Harrison. The slide (BM 23671) has unfortunately been damaged by someone circling the specimen of *P. angulatum* and this has caused a perforation in the coverslip which has led to the slide drying out.

The taxon described by McCall (1933) as *Pleurosigma angulatum* var. *robustum* (Fig. 2d) is subsumed under the name *P. angulatum* as no morphological differences can be found.

### MATERIAL EXAMINED

**UNITED KINGDOM. England.** Hartlepool, n.d., Arnott 570, Greville Coll. (BM 96); sine loc., n.d., Wm. Smith 2, Greville Coll. (BM 204); Hull, 1856, G.N. s.n., Greville Coll. (BM 386); Blyth Harbour, November 1857, Donkin C. No. 1, Greville Coll. (BM 389); Harwich, n.d., Anon. Deby Coll. (BM 7251); Harwich, n.d., Anon. Deby Coll. (BM 7253); Hull, n.d., R. Harrison 117, Deby Coll. (BM 11809); Hull, n.d., R. Harrison 117, Deby Coll. (BM 11810); sine loc., n.d., W.S. 205, Deby Coll. (BM 13331); Norfolk, n.d., F. Kitton 43, Deby Coll. (BM 13703); Poole Bay, August 1849, Anon., Wm. Smith Coll. (BM 23672); Pevensey, September 1851, Anon., Wm. Smith Coll. (BM 23674); Sussex, Ilford, April 1852, Anon., Wm. Smith Coll. (BM 23675); Sussex, Lancing, August 1852, Anon., Wm. Smith Coll. (BM 23676); Sussex, Seaford, December 1852, Anon., Wm. Smith Coll. (BM 23677); Pevensey, August 1853, Anon., Wm. Smith Coll. (BM 23679); Sussex, Newhaven, February 1854, Anon., Wm. Smith Coll. (BM 23681); Sussex, Southsea, August 1854, Anon., Wm. Smith Coll. (BM 23682); Sussex, Shoreham, April 1854, Anon., Wm. Smith Coll. (BM 23683); Sussex, Shoreham, April 1854, Anon., Wm. Smith Coll. (BM 23684); Essex, Walton, n.d., Comber 3 (BM 31459); Essex, Walton, n.d., Comber 2 (BM 31458); Den Marsh, May 1896, Comber s.n., (BM 31460); Den Marsh, May 1896, Comber s.n., (BM 31461); Kent, Broad Water, near chalk 'S.157, 326', n.d., Rylands s.n., (BM 48371); River Mersey, n.d., I. Hardmach 331, Rylands Coll. (BM 48441); River Mersey, n.d., I. Hardmach 331, Rylands Coll. (BM 48442); Hull, 1857, W 103, 331, Rylands Coll. (BM 48444); Humber, Hull, n.d., GN 103, Rylands Coll. (BM 49989); Humber, Hull, n.d., GN 103, Rylands Coll. (BM 49990); Humber, Hull, n.d., GN 103, Rylands Coll. (BM 49991); Humber, Hull, n.d., GN 103, Rylands Coll. (BM 49992); Lancaster, Salt pool, '(274)383', n.d., Rylands s.n., (BM 48593). **Scotland:** Fife, Tayport, Tents Muir, Brackish Burn, n.d., D.R. McCall s.n. (BM 83451); Tayport, mud scraping from brackish pool on links, 23 September 1916, ex A.W. Round s.n., J.R. Carter Coll. (BM 93648). **Northern Ireland:** Belfast, Queens Island, n.d., Arnott 655, Greville Coll. (BM 1648); Belfast, August 1849, Anon., Wm. Smith Coll. (BM 23671); Carrickfergus, August 1849, Anon., Wm. Smith Coll. (BM 23673).

**IRELAND.** Galway, July 1853, s.n., Wm. Smith Coll. (BM 23678).

**FRANCE.** sine loc. 'Diatomées de France', n.d., 33/2,3 Anon., (BM – Adams Coll.).

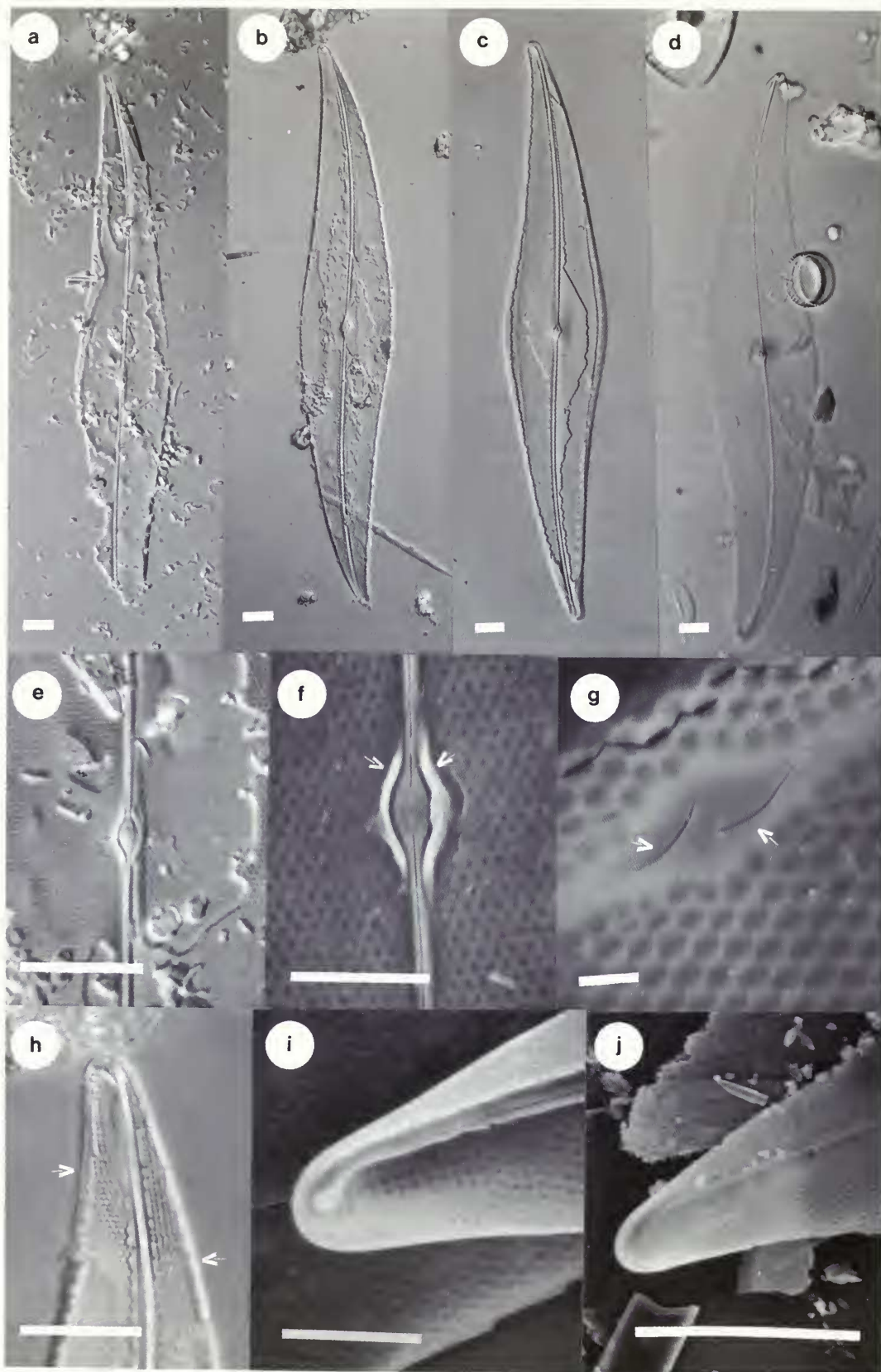
2. *Pleurosigma quadratum* W. Sm., in *A synopsis of the British Diatomaceae*. 1: 65 pl. 20 fig. 204 (1853). Type (designated here): England, Sussex, August 1850, Anon., BM 23669! (Isotype localities: Poole Bay; Coast of Sussex; Devonshire; Menai Straits; Folkestone).

Fig. 3

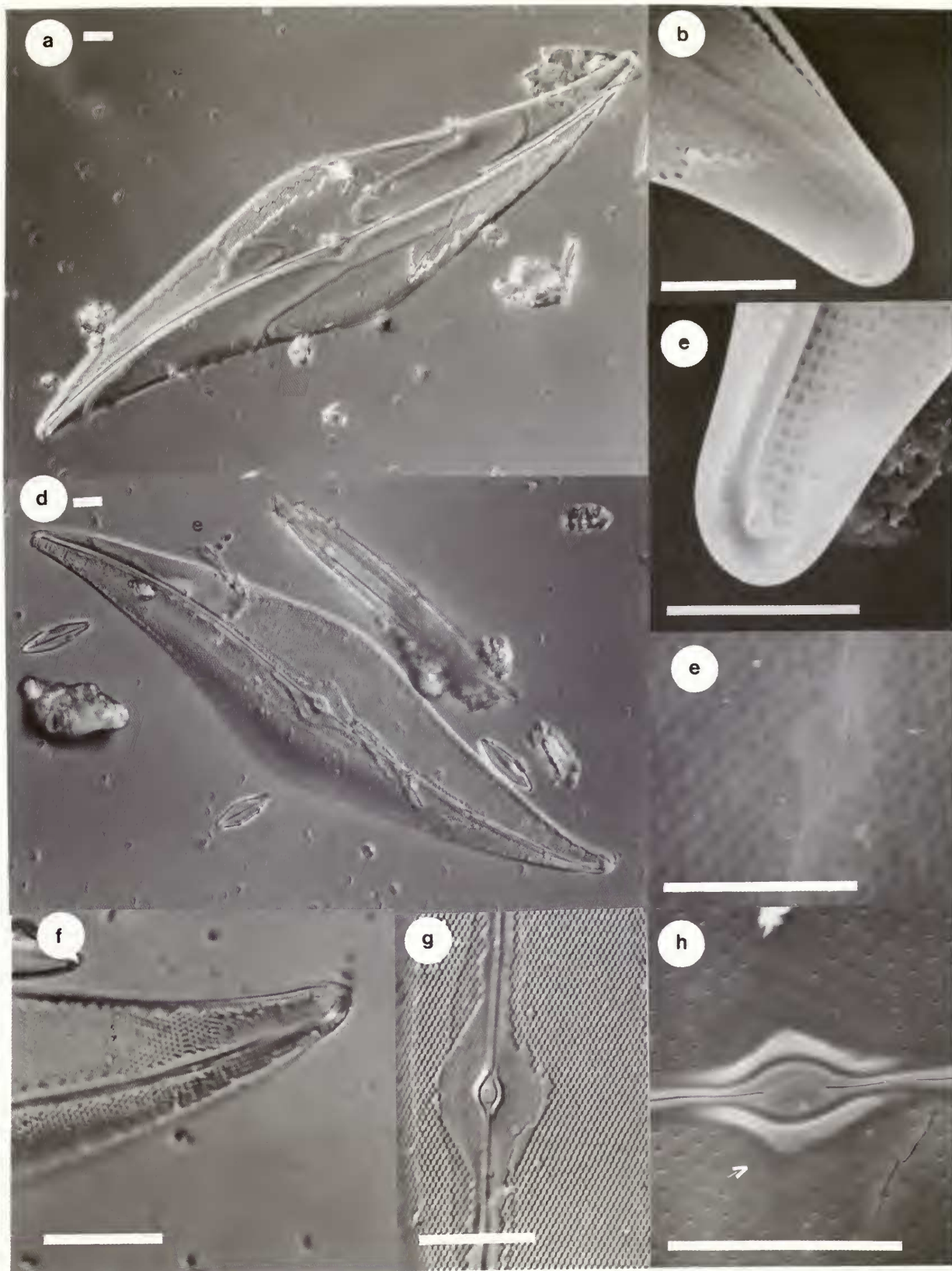
*Pleurosigma angulatum* W. Sm., *Ann. Nat. Hist.* 9: 7, pl. 1 fig. 7 & 9 (1852).

*Pleurosigma angulatum* var. *quadratum* (W. Sm.) Van Heurck, *Synopsis Diatomées Belgique*: 115 (1885).

Valves strongly rhombic, sigmoid, length 130–285 µm, breadth 50–65 µm (Fig. 3a, d). Raphe sigmoid eccentric towards the apices (Fig. 3a, d). Areolae undivided (Fig. 3c), transverse striae 19 per 10 µm,



**Fig. 2** *Pleurosigma angulatum*. (a) BM 23671; (b) BM 23674; (c) BM 386; (d) *P. angulatum* var. *robustum* (BM 83451); (e) light micrograph of central area (BM 23671); (f) SEM of internal central area, arrows indicating central bars; (g) SEM of external central fissures (arrows), one centred the other deflected; (h) light micrograph of valve apex showing change in striae orientation, arrows indicating the different distance of the striae change on either side of the raphe (BM 23674); (i) SEM of internal valve apex; (j) SEM of external valve apex. SEM micrographs from material of Wm. Smith Herbarium, Anon., Sussex, Lancing, August 1852. (Scale bars: a–e, h & j = 10  $\mu$ m, f & i = 5  $\mu$ m; g = 1  $\mu$ m).



**Fig. 3** *Pleurosigma quadratum*. (a) BM 23669; (b) SEM of external apex; (c) SEM of internal apex; (d) BM 23669; (e) SEM of external central area showing central raphe fissures; (f) light micrograph of valve apex showing change in striae orientation (BM 23669); (g) light micrograph of central area (BM 23669); (h) SEM of internal central area, arrow indicating hyaline area. SEM micrographs of Wm. Smith Herbarium material, *Anon.*, Sussex, August 1850. (Scale bars: a, d, f, g = 10 µm; b, c, e, h = 5 µm).

oblique striae 18 per 10  $\mu\text{m}$ , intersecting at an angle of 50–60°, changing orientation near the apex (Fig. 3b, c, f). External central raphe fissures one deviating to one side the other centred (Fig. 3e). Central bars of approximately equal length, thickened at the centre with an indistinct outer edge (Fig. 3g, h). Hyaline area follows central bars (Fig. 3h) in contrast to *P. angulatum* (Fig. 2f).

#### MATERIAL EXAMINED

**UNITED KINGDOM. England:** Harwich, n.d., *Arnott* s.n., Greville Coll. (BM 316); W. *Smith* 204, Greville Coll. (BM 219); Devon, Saltmarsh, n.d.,

*Gregory* s.n., Greville Coll. (BM 2129); Harwich, n.d., *A. Gr.* 814, Deby Coll. (BM 7108); Poole Bay, June 11 1849, *Smith* 204, Deby Coll. (BM 13320); Folkstone, November 1852, *J.R. Capron*, *Smith* 204, Deby Coll. (BM 13321); Norfolk, n.d., *F. Kitton* 43, Deby Coll. (BM 13703); test slide, sine loc., n.d., *Anon.*, Roper Coll. (BM 20751); Sussex, August 1850, *Anon.*, Wm. *Smith* Coll. (BM 23669); Hull, n.d., *Dr Ivl* 330/1, Rylands Coll. (BM 48384); Hull, n.d., *Dr Ivl* 330/2 Rylands Coll. (BM 48385); Northfleet (S. 750) 330, n.d., *Anon.*, Rylands Coll. (BM 88383); Harwich, Walton Ferry, n.d., *Anon.* 814, Rylands Coll. (BM 50436).

3. *Pleurosigma aestuarii* (Bréb.) W. Sm. in *A Synopsis of the British Diatomaceae*. 1: 65, pl. 31 fig. 275 (1853). Type: France, St Vaast, n.d., *de Brébisson* s.n., BM100839!

Fig. 4

*Navicula aestuarii* Bréb. in Kützing, *Species Algarum*: 890 (1849). *Gyrosigma aestuarii* (Bréb.) Griffith et Henfrey in *The Micrographic Dictionary*: 302, pl. 11 fig. 35 (1856).

Valves lanceolate, slightly sigmoid, apices rostrate (Fig. 4a). Length 60–90  $\mu\text{m}$ , breadth 12–20  $\mu\text{m}$ . Raphe central becoming eccentric towards the apices, strongly sigmoid. Internal central bars smooth and of equal length (Fig. 4b). Hyaline area absent from besides central bars (Fig. 4b). External central raphe fissures overlapping (Fig. 4d). Areolae not divided by a silica bar (Fig. 4b). Striae change orientation at the apex (Fig. 4c). Transverse and oblique striae 18 per 10  $\mu\text{m}$  intersecting at 60°.

#### MATERIAL EXAMINED

**FRANCE. St Vaast:** n.d., Kützing 1567 (BM 18866); n.d., Kützing 1729 (BM 18867); n.d., *de Brébisson* s.n., (BM 100839); n.d., *de Brébisson* s.n., (BM 100840).

4. *Pleurosigma mamoranqi* G. Reid *sp. nov.* Type: New Zealand, South Island, Mamoranqi Bay, n.d., *S.R. Stidolph* s.n., BM81613! Fig. 5

Valva rhombicus, sigmoideo, 100–120  $\mu\text{m}$  longa, 15–19  $\mu\text{m}$  lata. Raphe valde sigmoidea. Striae transapicales 26 per 10  $\mu\text{m}$ , striae obliquae 16 per 10  $\mu\text{m}$ . Poris habens transtrum. Transtra centralia laeves, in longitudine aequales, ovalis area hyalina.

Valves rhomboidal, sigmoid, length 100–120  $\mu\text{m}$ , breadth 15–19  $\mu\text{m}$  (Fig. 5a, h). Raphe strongly sigmoid and eccentric towards the apices (Fig. 5a, h). Areolae with a bar across them (Fig. 5c, e), transverse striae 26 per 10  $\mu\text{m}$ , oblique striae 16 per 10  $\mu\text{m}$ , intersecting at an angle of 56°, striae do not change orientation at the apex (Fig. 5d–g). Internal areolae of a different shape around the helictoglossa (Fig. 5e). External central raphe fissures overlapping (Fig. 5b, g). Internal central bars smooth, approximately equal in length (Fig. 5c). Hyaline area adjacent to the central bars oval (Fig. 5c).

#### MATERIAL EXAMINED

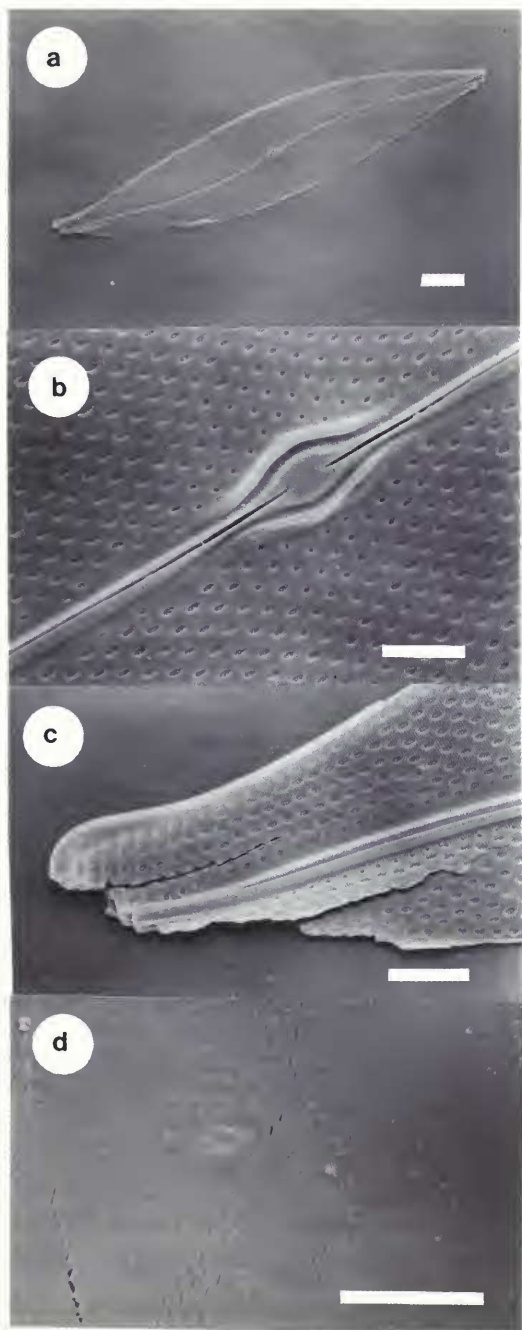
**NEW ZEALAND. South Island.** Mamoranqi Bay, n.d., *S.R. Stidolph*, BM81613.

5. *Pleurosigma lysekilii* G. Reid *sp. nov.* Type: Sweden, Lysekil, n.d., *P.T. Cleve* s.n., BM12896! (Cleve & Möller no. 142; Deby collection).

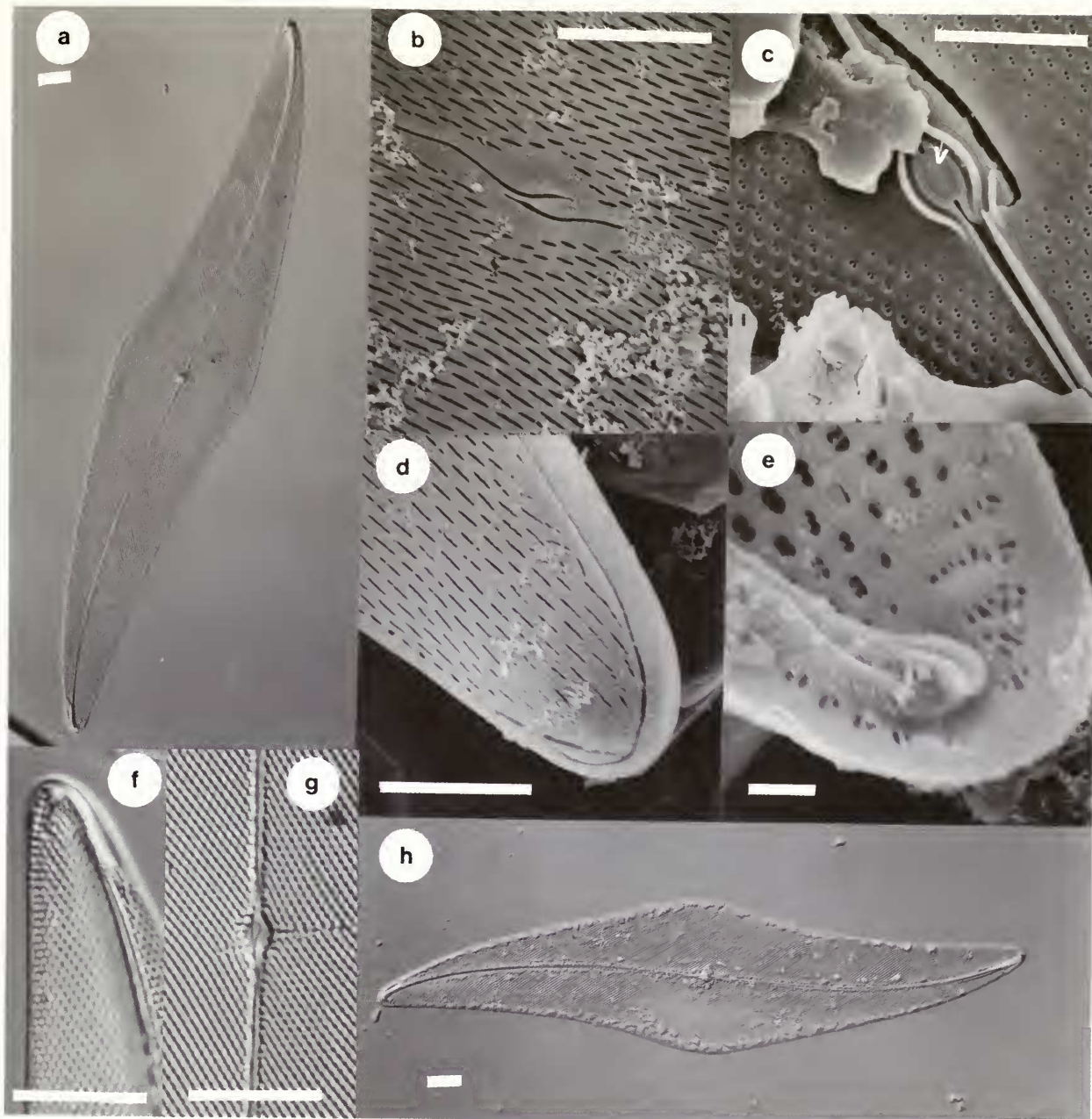
Fig. 6

*Pleurosigma angulatum* f. *minor* Cleve in Cleve and Möller, *Diatoms (exsiccata)* III: 4, no. 142 (1878) nom. nud.

Valva lanceolatus ambitu ita leviter sigmoideo. Raphe centralis leviter sigmoidea. 160–262  $\mu\text{m}$  longa, 20–30  $\mu\text{m}$  lata. Striae transapicales 17–19 per 10  $\mu\text{m}$ , striae obliquae 18–20 per 10  $\mu\text{m}$ .



**Fig. 4** *Pleurosigma aestuarii* (a) SEM of valve; (b) SEM of internal central area; (c) SEM of internal valve apex, showing change in striae orientation; (d) SEM of external central area. Material from letter of *de Brébisson* 27 February 1849 to Walker *Arnott*. (Scale bars: a = 10  $\mu\text{m}$ ; b, c = 2  $\mu\text{m}$ ; d = 5  $\mu\text{m}$ ).



**Fig. 5** *Pleurosigma mamoranqi*. (a) BM 81613; (b) SEM of external central area; (c) SEM internal central area, arrow indicating extra siliceous deposit in middle of central nodule; (d) SEM of external valve apex; (e) SEM of internal valve apex; (f) light micrograph of valve apex (BM 81613); (g) light micrograph of central area showing external central raphe fissures (BM 81613); (h) BM 81613. SEM micrographs from New Zealand, Momoranqi Bay, ex *Stidolph* 155. (Scale bars: a, f–h = 10  $\mu$ m; b, c = 5  $\mu$ m; e = 1  $\mu$ m).

Valves lanceolate, only slightly sigmoid at the apices, subacute (Fig. 6a). Raphe central sigmoid at the apices (Fig. 6a). Length 160–262  $\mu$ m, breadth 20–30  $\mu$ m. Transverse striae 17–19 per 10  $\mu$ m, oblique striae 18–20 per 10  $\mu$ m, crossing at 58–61°. No change in the orientation of the striae at the apex (Fig. 6b) in contrast to *P. angulatum*. Central area small (Fig. 6b).

The name *Pleurosigma angulatum* f. *minor* Cleve and Möller cannot be applied to this taxon as it has prior use, *Pleurosigma angulatum* f. *minor* Rabenh. (1864). The taxon is not a form of *angulatum* in that it does not possess striae that change orientation at the apex.

#### MATERIAL EXAMINED

**SWEDEN.** Lysekil, n.d., *P.T. Cleve* s.n., Cleve & Möller no. 142, Deby Coll., (BM 12896); 'W.Göteborg, Bahus', n.d., *P.T. Cleve* s.n., Cleve & Möller no. 142, Wynne Baxter Coll. 5342 (BM 59695).

6. *Pleurosigma malmöensis* G. Reid *nom. nov.* Type: Sweden, Malmö, n.d., *M.O. Nordstedt* s.n., BM 12902! (Cleve & Möller no. 136, Deby Collection).

Fig. 7

*Pleurosigma aestuarii* var. *minutum* Grunow in Cleve and Möller *Diatoms (exsiccata)* III: 3, no 136 (1878).

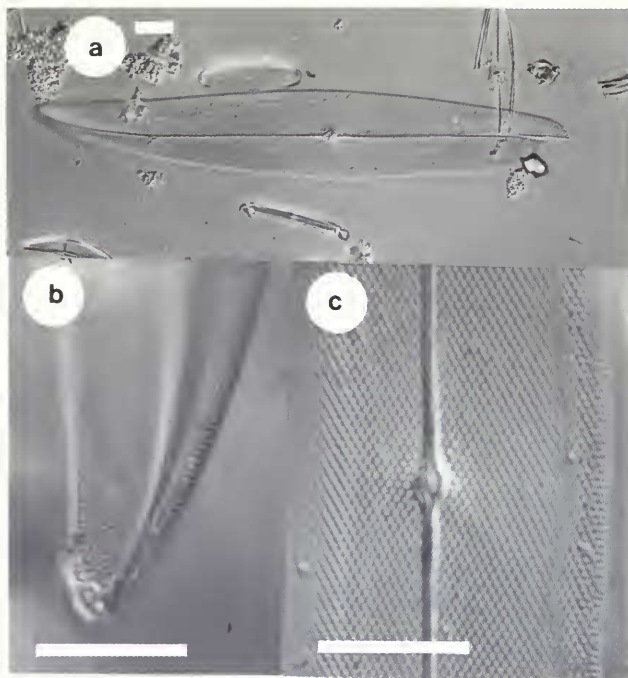


Fig. 6 *Pleurosigma lysekilii*. (a) BM 12896; (b) valve apex; (c) central area. (Scale bars: a–c = 10  $\mu$ m).



Fig. 7 *Pleurosigma malmoensis* BM 12902. (Scale bars: a–b = 10  $\mu$ m).

*Pleurosigma minutum* (Grunow) Cleve, Kong. Sven. Vet. Hand. 26: 41 (1894).

*Pleurosigma angulatum* f. *minutum* (Grunow) De Toni, Syll. Alg.: 232 (1891).

*Pleurosigma angulatum* var. *minutum* (Grunow) McCall, J. Linn. Soc. Lon. Bot. 49(328): 266 (1933).

Valves sigmoid, lanceolate, length 50–75  $\mu$ m, breadth 12–15  $\mu$ m (Fig. 7). Raphe central, sigmoid (Fig. 7). Transverse striae 26–27 per 10  $\mu$ m, oblique striae 28–29 per 10  $\mu$ m, crossing at an angle of 60°. Central area small with smooth central bars of approximately equal length, there is no hyaline area adjacent to the central bars. External central fissures curved in the same directions (Fig. 7a). Striae do not change orientation at the apex (Fig. 7).

#### MATERIAL EXAMINED

SWEDEN. Malmö: n.d., *M.O. Nordstedt* s.n., Cleve & Möller. no. 136, Deby Coll. (BM 12902); n.d., *M.O. Nordstedt* s.n., Cleve & Möller no. 136 (BM – Adams Coll.).

7. *Pleurosigma stidolphii* Sterrenburg, Bot. Mar. 34: 568, figs 38–46 (1991). Type: New Zealand, Otago Harbour, October 1961, A.J. Doig s.n., BM81608!

Fig. 8

Valves very rhombic, sigmoid, tapering to acute apices. 100–270  $\mu$ m long; 30–60  $\mu$ m wide (Fig. 8a). Valve vaulted with raphe situated on a ridge (Fig. 8a). Internal central bars with siliceous lateral extensions. Central area small (Fig. 8c). Oblique striae 22–25 per 10  $\mu$ m;



Fig. 8 *Pleurosigma stidolphii* BM 81608. (Scale bars: a–c = 10  $\mu$ m).

transverse striae 23–27 per 10 µm. Striae do not change orientation at the apex (Fig. 8b). Areolae undivided. External central raphe fissures overlapping.

#### MATERIAL EXAMINED

**NEW ZEALAND.** Otago Harbour, October 1961, A.J. Doig s.n., leg. S.R. Stidolph (BM 81608).

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